

Intergroup Interactions in Tibetan Macaques at Mt. Emei, China

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KEY WORDS close encounter; fission; food competition; long-distance interaction; *Macaca thibetana*; sexual attractiveness; sexual selection

ABSTRACT Data on intergroup-interactions (I-I) were collected in 5 seasonally provisioned groups (A, B, D, D₁, and E) of Tibetan macaques (*Macaca Thibetana*) at Mt. Emei in three 70-day periods between 1991 April-June (P1), September-November (P2), December-1992 February (P3). The I-I were categorized as forewarning made by high-ranking males (including Branch Shaking and/or Loud Calls), long-distance interactions in space (specified by changes in their foraging movements), and close encounters (with Affinitive Behavior, Male's Herding Female, Sexual Interaction, Severe Conflict, Adult Male-male Conflict, Opportunistic Advance and Retreat, etc. performed by different age-sex classes). From periods P1 to P3, the I-I rate decreased with reduction in population density as a positive correlate of food clumpedness or the number of potential feeders along a pedestrian trail. On the other hand, from the birth season (BS, represented by P1 and P3) to the mating season (MS, represented by P2) the dominance relation between groups, which produced a winner and a loser in the encounters, became obscure; the proportion of close encounters in the I-I increased; the asymmetry (local groups over intruders) of forewarning signals disappeared; the rate of branch shaking decreased; and sometimes intergroup cohesion appeared. Considering that sexual interactions also occurred between the encountering groups, above changes in intergroup behaviors may be explained with a model of the way in which the competition for food (exclusion) and the sexual attractiveness between opposite sexes were in a dynamic equilibrium among the groups, with the former outweighing the latter in the BS, and conversely in the MS. Females made 93% of severe conflicts, which occurred in 18% of close encounters. Groups fissioned in the recent past shared the same home range, and showed the highest hostility to each other by females. In conspicuous contrast with females' great interest in intergroup food/range competition, adult male-male conflicts that were normally without body contact occurred in 66% of close encounters; high-ranking male herding of females, which is typical in baboons, appeared in 83% of close encounters, and showed no changes with season and sexual weight-dimorphism; peripheral juvenile and subadult males were the main performers of the affinitive behaviors, opportunistic advance and retreat, and guarding at the border. In brief, all males appeared to "sit on the fence" at the border, likely holding out hope of gaining the favor of females both within and outside the group. Thus,

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females and males attempted to maximize reproductive values in different ways, just as expected by Darwin-Trivers' theory of sexual selection. In addition, group fission was observed in the largest and highest-ranking group for two times (both in the MS) when its size increased to a certain level, and the mother group kept their dominant position in size and rank among the groups that might encounter, suggesting that fission takes a way of discarding the "superfluous part" in order to balance the cost of competition for food and mates within a group, and the benefit of cooperation to access the resources for animals in the mother group. *Am J Phys Anthropol* 104:459–470, 1997.

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Female residence and systematic movement of males among groups occur in macaques and many other primate species. The social unit of such species is typically "female-bonded," i.e., composed almost entirely of female kin and immigrant males (Wrangham, 1980). The social group of Tibetan macaques (*Macaca thibetana*) belongs to this category (Zhao, 1994a).

Group living in primates has been proposed to be selected to enhance the success of individuals in defense of limited resources such as food, water, and sleeping sites, thus the intergroup relationship is essentially competitive (Wrangham, 1980). However, if the diameter of the home range of a primate group is larger than the average distance covered daily, the group is likely to share its range, at least partly, with other groups (Mitani and Rodman, 1979). When home-range overlap is great, as it typically is in macaques, aggressive encounters occur at low rates, and those that do occur usually concern access to a clumped resource, such as that at human provisioning sites. Away from such resources, macaque encounters generally involve passive avoidance (Southwick et al., 1965; Kawanaka, 1973; Lindburg 1977).

Intergroup competition for resources is often mediated by the relative dominance ranks of the groups involved. Dominance among macaque groups is usually a function of group size, or the number of adult females (Wrangham, 1980). Occasionally, however, it may depend on more subtle factors, such as past relations among the male members of different groups in rhesus macaques (Gabow, 1972).

In most mammalian species, females have to channel more energy to offspring than do

males, and their reproductive success appears limited primarily by food acquisition related to the foraging range. In contrast, male reproductive success is limited mainly by the availability of females (Darwin, 1871; Trivers, 1972). This is the essence of sexual selection theory. Accordingly, such a sex difference is expected to be embodied in the performances of females and males in intergroup interactions. That is, a) females should tend to engage in intergroup food/range competition more actively and seriously than males, and b) males should try their best to gain the favor of females both within, and outside the group for additional mates immediately or in consideration of smoothing later transfer.

In studies on primate intergroup interactions, the aspect of competition for food/range has been emphasized (see Cheney, 1987), but little attention was paid to the opposite—the force contended against the exclusion—though sexual attraction to unfamiliar opposite sexes is commonly observed in non-human primates (Enomoto, 1974; Sugiyama, 1976; Cheney and Seyfarth, 1977; Brereton, 1981; Hausfater, 1972; Zhao, 1993) and in humans (Shepher, 1971; Wolf and Huang, 1980), and male reproductive strategies have recently been suggested to govern intergroup relationships in baboons (Cowlshaw, 1995).

At the Mt. Emei site, the Tibetan macaque groups are living under an unintended natural (unplanned) experimental condition with exaggerated seasonal changes in food availability and clumpedness due to provisioning. This, together with the directional movement of potential feeders, to which the macaque groups response in a way of moving in the opposite direction (Zhao, 1994c),

and the involvement of as many as 5 groups afford a rare opportunity to inspect the current selective pressures on the social group of Tibetan macaques, a previously little known species. This study was planned to approach this important but poorly documented topic through analyses of a) the relation of intergroup interaction rates to food clumpedness, b) the behavior of males and females during intergroup interactions, and c) demographic data in relation to group fission and the interactions between fissioned groups.

METHODS

The study site is mainly between 1,500–2,400 m on the northeast slope of Mt. Emei (29°30'N and 103°19' for the summit) rising from 500 m to 3,099 m a.s.l. The forest habitat of study groups is usually snow-blanketed for 3.5 months per year, and the mean temperature in January is -1.3°C at 2,070 m (Zhao, et al., 1989).

The macaques that range in or near the tourist and Buddhist center, depend on both food handouts and natural foods—foliage in spring and summer, and bamboo shoots and fruits in autumn—in the tourist or warm seasons, and otherwise, rely basically on foliage (Zhao et al., 1991). Seasonal provisioning from tourists and Buddhists has considerably exaggerated the periodical fluctuation of food availability and clumpedness, and made the macaque groups spend more and more time foraging along the trail. Because visitors enter the trail from either the upper (2,400 m) or lower (750 m) end, 10 groups ranged along the trail depending their intergroup rank in access to the feeders, and categorized as high, middle, and low groups (Zhao, 1994d). The study groups (A, B, D, and D₁) were those resident in the high part of the site, dominant over the middle groups, tending to forage daily by competitively moving upwards toward the descending trailgoers (Zhao, 1994c). Sometimes group E, one of the low groups (also dominant over the middle groups), moved through the middle, and had interactions with the groups B and D₁.

Quantitative data on intergroup interactions were collected between 0800 h–1700 h each day in three successive 70-day periods in the spring and summer (P1; April 15–

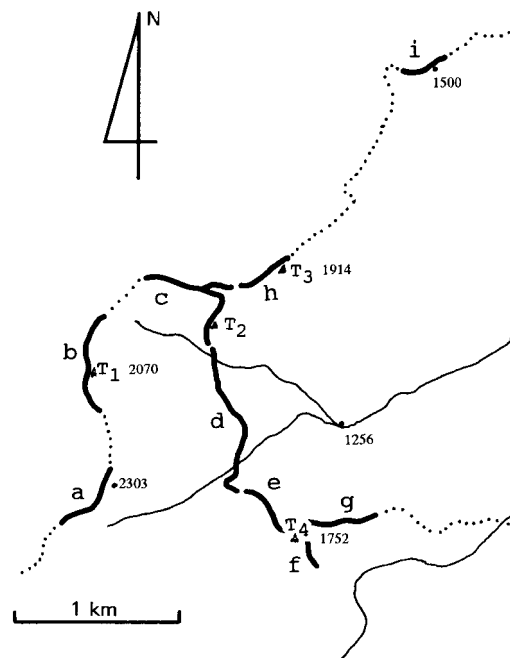


Fig. 1. Trail sections used by the study groups ranging at the upper part of the population range. Keys: used (thick lines a–i) and unused (dot lines) trail sections, temples visited by the groups (T_{1–4}), streams (thin line), and elevation above sea level in meters (four-digit number).

June 23, 1991), autumn (P2; September 1–November 9, 1991), and winter (P3; December 1–February 8, 1991/2). In the three periods, groups B, D, and D₁ were radio-tracked. Over the seasons, the potential human feeders were present in thousands each day in spring and summer, but only in hundreds daily in autumn, and tens daily in winter.

P3 and P1 can be used to represent the birth season (Zhao, 1994d), in which the macaques are sexually inactive. Within the birth season, the availability of human-provided food along the trail reaches its annual peak between May and August, but falls in the annual valley in winter. P2 falls in the middle mating season, in which sexual activities both within and between groups reaches the peak, but the availability of human-provided food falls between P1 and Ps.

Data on intergroup encounters include those observed between/among five groups (A, B, D, D₁, and E) when they entered the regular observation areas (trail sections c, d,

e, *f*, *g* in Fig. 1), the groups' activity center. Survey routes were usually taken according to the following schedule: if any of the groups B, D₁ and E appeared at sections *e*, *f*, and *g* near temple T₄, my camp, I stayed there with one of the groups (but not more than three successive days for one group), then changed to another group. After working in this area, I moved to follow the groups in sections *c* and *d* (A, B, D and D₁) in the same way. Other sections (*a*, *b*, *h*, and *i*) were also surveyed, but not regularly. With the aid of the radio-tracking system, some of the long-distance interactions among groups B, D, and D₁ were determined by checking their daily ranging routes. Following the survey program, the relative rate of close encounters and long-distance interactions (see below) should be comparable across the sampling periods.

The occurrence of a particular behavior was scored as 1 when it occurred at least once in the course of an interaction, and otherwise as 0. Because not all encounters were fully observed, the one-zero scores probably described the occurrence of these behaviors more accurately than the exact frequencies recorded in the course of imperfectly observed encounters. On the other hand, the observation duration for close encounters showed no difference between the birth and mating seasons (2.4 vs. 2.9 h, $t = -0.75$, $P > 0.05$), and the occurrence rate of behaviors is likely to be comparable between the seasons.

Taking advantage of the fact that the groups regularly moved up along the trail to meet the tourists going down and carrying food (Zhao, 1994c), the outcome of inter-group food competition was simply inferred from the groups' foraging movements. That is, the dominant group controlled the trail or the higher section, and the loser was driven away from the trail or remained in the lower part.

Because I did not always arrive at the beginning of the interactions, and the encountering groups sometimes soon disappeared in the forest/cliff, sampling sessions used in data processing include relatively complete observations only for either warning phases or later encounters (see below). In addition to the quantitative data on the

interactions, some conspicuous events occurred outside the sampling periods are also integrated in this analysis for a full view of the encounters.

DEFINITIONS

Forewarning

These display patterns consisted of branch shaking and/or special long-loud calls (spectrographs in prep), often directed by alpha males to an opposing group at a distance of hundreds or tens of meters. Between two groups in interaction, forewarning signals might be uttered by one group or exchanged by the two. Forewarning might or might not appear at the beginning of interactions described below.

Long-distance interactions

In these interactions, one group's foraging movement was influenced by another group at a distance of hundred or tens of meters. In this category, a group might stop below a trail section occupied by a higher-ranking group, sometimes for days; go back down along the trail or through the forest when a higher-ranking group was detected at a higher position, or moving in the opposite direction; enter a trail area after the higher-ranking group fully left (for example, 30 min later), leave a contested area, to which a dominant group was moving, or retreat to an area that was exclusively used by the group.

Close encounters

Situations in which two or three groups were in physical contact or separated by a distance of less than 10 m, either seen clearly at the trail or judged to be in direct contact by the observer's hearing special fighting calls. This pattern might last for up to 5 h.

Border

In close encounters, an imaginary line might be put between animals from different groups. Because home ranges overlapped extensively, the border was a moving or soft one (see Opportunistic advance and retreat) in any part of the range. It was also the place for the observer to collect data on the encounter.

Affinitive behaviors

At the border, animals from different groups made present, mount, mouth-mouth contact, penis look (in which a male took the presenter's penis and looked at it for a short time), and contact threat [in which the dominant grasped at another animal that actively presented/exposed the body part with submissive face expression, and lightly bit its front part of body, or grasped at head hair and then made an attack face (Bertrand, 1969) at the latter]. In intragroup interactions, these affinitive behaviors, especially the contact threat, usually resulted in a decline of social tension between the animals, reflected for example in the toleration of a subordinate in proximity or feeding nearby.

Herding

Males tried to counter-chase or drive their own females in order to keep them away from the border. Females usually ran backwards and waited to return to the border again when the herder was out of view, but the situation was different in severe conflicts (defined below).

Sexual interaction

Sexual behaviors occurred between animals from different groups, consisting of sexual initiation (bared teeth chatter of males, lifting female's hip, female's presenting), and mating (mount, intromission, and pelvic thrust and/or ejaculation). Because this species is a multiple-mount-to-ejaculation species, mounting might or might not result in ejaculation (Zhao, 1993). This type of interaction was observed only in the mating season.

Severe conflict

If males failed to herd females, and most of a group's members took part in an encounter seriously, this category was scored. Such conflicts, which might result in wounding and/or more severe consequences (described below), were always accompanied by high-pitched calls uttered mainly by female fighters of both sides, and lasting up to 2.5 h.

Adult male-male conflict

A burst of violent male-male chasing, accompanying a string of short-loud "co-co-co..." calls (spectrographs in prep) uttered by the attacker. Usually, only two or three males (excluding the very low-ranking ones) from different groups were involved in such local fights, which never resulted in wounding.

Opportunistic advance and retreat

Silent actions at the border, in which an outnumbered group retreated when an opposing group was strengthened by one or two newcomers. The movement was reversed if the retreating group received reinforcements that reversed the balance. The seesaw battle was mainly made by juvenile and subadult males, and might be repeated many times in a regular close encounter.

Intergroup dominance

If a close encounter resulted in a group's retaining possession of, or displacing another group at, a favorite trail section, the keeper or displacer was defined as the winner, the other was the loser. Otherwise, the close encounter resulted in uncertainty. From the tally of wins and losses, the intergroup dominance hierarchy could be determined.

Intruder and resident

If a group came into a close encounter with another group that appeared earlier at a trail section, the later comer and the early one were defined as the intruder and resident respectively.

RESULTS

Two groups came into interactions with each other in a distance of hundreds or tens of meters when the foraging movement of any one group appeared to be influenced by another. A forewarning phase sometimes appeared at the beginning, and the groups might stay in long-distance interactions for up to days, or proceed to a close encounter, in which behaviors such as those listed above occurred. At the end, a close encounter might result in a winner and a loser, or in uncertainty.

TABLE 1. Distribution of long-distance interactions (LDI) and close encounters (CE) observed in five groups of seasonally provisioned Tibetan macaques in three 70 day periods in spring-summer, autumn, and winter respectively

Season	LDI				CE			
	A	B	D	D ₁	A	B	D	D ₁
Spring & summer (1991)								
A								
B	2				1			
D		13				4		
D ₁	2	11	19			6	3	
E		3		7		3		2
Total		(57)				(19)		
Autumn (1991)								
A								
B	3				1			
D		2			6	1		
D ₁	1	3	15			9	12	
E				3		2		1
Total		(27)				(32)		
Winter (1991/2)								
A								
B								
D					3		1	
D ₁	3	1	5		3			
E								
Total		(9)				(7)		

Behavioral changes with season

The rate of long-distance interactions (LDI) plus close encounters (CE) (Table 1) was significantly different in spring-summer (1.09/day), autumn (0.84), and winter (0.23) (F -ratio = 31.04; df = 2, 207; P < 0.001). In fact, the rate progressively decreased with reduction of food clumpedness (described with the number of potential feeders) over the seasons.

On the other hand, the ratio of CE/LDI changed from 19/57 in P1 (spring-summer), to 32/27 in P2 (autumn), to 7/9 in P3 (winter). The ratio of CE/LDI was 13/33 or 26/66 (combination of P1 and P3) in the birth season and 32/27 in the mating season, and the change between the two seasons was significant (Proportion Test for CE/(CE + LDI): z = -3.20, P < 0.001).

Branch shaking appeared more often in the birth season than in the mating season (Table 2a). The resident groups tended to produce forewarning signals (branch shaking and/or long-loud calls) more often than the intruder in the birth season, but not in the mating season though the asymmetry was retained in the year. In addition, the asymmetry became stronger if both branch

shaking and loud-calls were considered (Table 2b). Interestingly, 90% of 21 observed bouts of branch-shaking were made by alpha-males, 1/5 of the actions with long-loud calls. Of 7 forewarning phases with calls, 5 did not develop into close encounters.

Sexual interactions between animals from different groups were observed in 6 of 14 close encounters in the mating season, and none in the birth season. The sexual behaviors included 9 matings (1 ejaculation) and 16 initiations (8 bared-teeth chatters and 2 lifting female's hip of males, and 6 presenting actions of females). Of the mounts, only one was made by an alpha male, and the ejaculation was made by a subadult male (Table 2c).

A dominance hierarchy was observed in 16 close encounters (Table 3) in four groups in the birth season. Obviously, the rank order for groups that met each other was $D > A > B > D_1$. However, the clear dominance relations became obscure in the mating season (outcome in Table 2c).

Taking advantage of the changes appeared in the mating season, group D_1 peacefully made its first range extension into group B's range three years after its fission from group D in September, 1991.¹

It is of interest to note how a rank-reversal between groups A and B occurred. In the 1986 birth season, group B was dominant over group A under the condition that there were 8 females (F), 4 males (M), 2 subadult males (SA) in A [group size (gs) = 24], and 10 F and 5 M in B (gs = 30, Zhao and Deng, 1988). At the end of 1987, all 5 adult males of group B were former members of group A. Of the five, two young adult males Ne and Ni natively transferred in the 1987 mating season, and two middle-aged males Ha and Ey transferred after losing their alpha positions in 1985 and 1987 respectively. After the replacement of males in group B, Ni became the alpha, Ne also rose

¹Mediated by one of two transferring males from D_1 to B, a higher-ranking group. D_1 followed B moving around T_4 (Fig. 1), where food handouts were relatively rich and D_1 had never arrived, for 3 days on 6–8th without conflict. In the period, D_1 always followed B in a distance less than 10 m, foraging at trail-sections e, g, and f or in the forest; sexually active animals from different groups kept trying to have sexual interactions during the day. D_1 even kept following B to its sleeping site in late afternoon. After the exploration, D_1 began to range in the area around T_4 regularly.

TABLE 2a. Seasonal changes in scores of forewarning behaviors in intergroup interactions in five groups of Tibetan macaques at Mt. Emei¹

Season (S.)	Branch shaking				Long-loud call			
	Resident	Intruder	Both	Total	Resident	Intruder	Both	Total
Birth S. (n = 18)	10	2	1	13	4	0	1	5
Mating S. (n = 12)	3	1	1	5	0	0	2	2
Aver. rate of two S. (%)	40	10	7	57	11	0	11	22
Difference between S. ² (z)				1.7**				NS

¹ 1 was scored when a behavior occurred in sampling period, otherwise, 0.

² Proportion test: ** $P < 0.01$; NS = $P > 0.05$.

TABLE 2b. Seasonal changes in asymmetry of forewarning behaviors presented in Table 2a (proportion test for difference between local groups and intruders, z-values and probability)^{1,2}

Season (S.)	Branch-shaking (BrS)	Long-loud call (LC)	BrS & LC
Birth S.	2.74**	1.79*	4.03***
Mating S.	0.94	0.00	0.83
Both S.	2.74**	1.39 (NS)	4.14***

¹ The score in 'Both' column of Table 2a is added to scores for the resident and the intruder.

² * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in rank (Zhao, 1994a), and A became dominant over B although the demographic variables remained as $B > A$ (7F and 4M in A; 8F and 6M in B; size A/size B = 29/36 in the middle of the 1987 mating season; Zhao 1993). The dominance of A over B continued to the end of 1991 even though a new immigrant from group D took the alpha position of B when Ni and Ne died of dropping down a large cliff accidentally and Ey disappeared in the icy December of 1990, and the size ratio further decreased to 17/27.

Behaviors not changing with season

Males herding females at the border occurred in 83% of close encounters, but showed no difference between the BS and the MS (Table 2c, Proportion Test, $z = -0.41$, $P > 0.05$). Ninety-one of 133 herding actions were made by alpha males towards their adult females.

Severe conflicts, which mainly involved females, occurred in 18% of close encounters. On the other hand, chasing between adult males from different groups occurred in 66% of close encounters (Table 2c). In addition, no intergroup male-female aggression were observed in this study. Different

roles of females and males in the fight can be clearly seen.²

The peripheral males (mainly the juvenile, subadult) were the most active elements in affiliative performances, opportunistic advance and retreat (Table 2c), and in guarding at the border in normal close encounters. In one case, a subadult male was forced to be a guard at the border.³

Group fission and interactions between fissioned groups

Group fission was noted in the largest and most dominant group (D) twice during the study period between 1986–1992. The fissions occurred when group size reached 79 in 1988, and 61 in 1991 respectively. Both occurred in the mating season. In addition, the majority or the mother group (67 and 43 respectively) kept its dominant position in both size and rank among the groups—the

²On April 15, 1989, at 1300 h, 2 dominant adult females (with an infant) and a subadult male from group D₁ faced, at a distance of about 5 m, 2 mother-infant pairs and another female from group D, about 7 m above section d (Fig. 1). Later, the alpha and beta males of D₁ arrived, and began to herd their females but failed to drive them away from the contact zone. The females kept brandishing or moving one hand up and down in the direction of opposing females at a distance less than 1 m, uttering a lot of high-pitched calls. The females' fight and D₁'s male herding dislodged a lot of soil and stones from the slope. At 1418 h, 3 more females from D joined the fight, and 6 females with 3 infants formed a small wall at a higher position. Ten minutes later, when two adult males appeared behind the females of D, a general attack from females of D began, and the border soon moved down to the deep valley where the noisy calls lasted for 30 min. The severest intergroup conflict resulted in (in addition to about 120 kg of fallen soil and stones remaining on the trail) an infant's disappearance and the beta male's transferring from group D₁. Interestingly, a low-ranking female and a subordinate male from group D₁ were not involved in the fight.

³On May 5th, 1986, 1245 h after two bursts of male-male conflicts in the forest, the alpha male of group F forced a subadult male to go backwards to the 'border' for about 15 m. When moving backwards, the subadult faced the driver and grimaced repeatedly. When the subadult reached the border and climbed into a tree, the alpha male retired to a point about 25 m away from the border. The subadult kept watching and sometimes made lunge threats to his opponent for 30 min. At 1345 h, one more male-male conflict occurred in the forest, but the guard at the border seemed to be oblivious of the fight until C disappeared at 1400 h.

TABLE 2c. Seasonal changes in occurrences of behaviors in close encounters¹

Season (S.)	Adult female at border			Alpha male at border			Opportunistic advance & retreat		Male-female conflict		Female-female conflict		Herding		Intergroup sex		Outcome	
	One side	Both sides	Total	One side	Both sides	Total	Affinitive interaction	Total	Male-female conflict	Male-female conflict	Female-female conflict	One side	Both sides	Total	Initiation	Mating	Winner	Uncertain
Birth S. (n = 15)	4	10	14	3	11	14	9	11	9	10	1	7	5	12	0	0	15	0
Mating S. (n = 14)	2	11	13	4	10	14	9	13	10	6	4	6	6	12	6	4	3	11
Average rate of two S.	21	72	93	24	72	96	62	83	66	18	18	45	38	83	NS	NS	—	—
Difference between S ²			NS			—	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	15.8***	(X ²)

¹ See footnote 1, Table 2a.² z (proportion test); NS, not significant; X² (crosstab); *** P < 0.001.

size of the second largest group (B) in the area was 40 and 27 respectively, and that of the second highest-ranking group (A) was 33 and 17.

Daughter group 1 (D₁) was composed of 1 middle-aged M, 3 F, and 8 immatures; and daughter group 2 (D₂) was of 1 young M, 1 SA, 8 F, and 8 immatures.

Within 2–3 years after group fission, the smaller daughter groups shared the original range with the larger one, but often took the lower/poorer trail sections, some of which were abandoned by the group before fission (Fig. 1 and Table 4). For example, group D₁ ranged usually at either section *d* or the lower *g* (using the forest between the two sections as passageway) when D was at *c*, otherwise, it would soon move to the best feeding site (*c*). Then the minority D₂ repeated the same ranging pattern with D₁: it regularly ranged at or between sections *c* and *i* depending on the majority D's presence or absence at section *c/d/h*—if D arrived at or approached *c/d/h*, D₂ usually took a long trip through the north-east forest to section *i*, otherwise D₂ soon returned to *c*. Note in particular that both *g* and *i* were given up by the un-fissioned group D, and the distance between *i* and *c/d/h* was far beyond the range of human senses.

In competition for limited resources within the range, females from one part showed an extremely high hostility to those from the other. Of a few severe female-female conflicts noted in the study periods since 1986, the most acute fights were observed between the majority (D) and the minorities (D₁ and D₂), 6 and 2 months after the fissions respectively.

DISCUSSION

The rate of intergroup interactions decreased from 1.09/day in spring-summer, to 0.84 in autumn, and to 0.23 in winter when the population density changed from 44/km² to 32 to 20 respectively (Zhao, unpublished data), or when the number of potential feeders decreased from thousands per day to hundreds to tens. The relation between population densities and interaction rates is expected by Waser's (1976) 'gas' model.

TABLE 3. *Intergroup dominance and group composition observed mainly in the 1991 birth season*

Winner-loser ¹ (n)	A-D ₁ (1)	B-D ₁ (6)	D-D ₁ (2)	E-D ₁ (2)	A-B (1)	D-B (3)	D-A (1)
Number of adult females	7-6	8-6	25-6	10-6	7-8	25-8	25-7
Number of adult & subadult males	4-4	6-4	9-4	5-4	4-6	9-6	9-4
Number of adults	11-10	14-10	34-10	15-10	11-14	34-14	34-11
(Intergroup rank order: D > A > B > D ₁)							

¹ No reverse was observed in the sampling period; the interaction between D and A occurred on December 1, 1989.

TABLE 4. *Changes in trail-range use in groups B and D, and the trail sections ranged by fissioned minor groups D₁ and D₂*

Group	Beginning ¹	1991/1992	
		Extended in	Giving up
Group B	<i>b c d f g h</i>	<i>a e</i>	<i>b h</i>
Group D	<i>c d g h i</i>	<i>b</i>	<i>g² i²</i>
Group D ₁	<i>c d g² h</i>	<i>e f</i>	
Group D ₂	<i>c i²</i>		

¹ Data collected in 1986 for groups B and D; groups D₁ and D₂ were fissioned from group D in October 1988 and late August 1991 respectively.

² Trail-sections given up by group D before the fissions.

Competition for food was mediated by the relative dominance rank between groups involved, just like the interaction among individuals within a group (Deng and Zhao, 1987). The intergroup dominance, however, was not simply determined by demographic variables such as adult females, adult males, total adults, or group size. The rank-reversal between groups A and B showed that more subtle factors such as past relations among males and experiences of females being with the males might influence the intergroup rank order, as in rhesus macaques (Gabow, 1972) and red colobus (Struhsaker and Leland, 1979; but see Cheney, 1987).

Forewarning is very likely to function as an advertisement of the group's presence that may discourage an intruder in the birth season, as similar behavior does in mantled howler monkeys (Chivers, 1969) and capuchins (Terborgh, 1983). Because most macaques seem to lack specialized intergroup calls (Cheney, 1987), the forewarning behavior observed in Tibetan macaques may be stimulated by the high intensity of competition for human food in the tourist season.

With the change in sexual activity (of intra- and intergroup) from absence in the birth season to presence in the mating sea-

son, the proportion of close encounters in total interactions increased, intergroup dominance became obscure, the asymmetry of forewarning behaviors (resident groups over intruders) disappeared, the rate of branch shaking decreased, and sometimes intergroup cohesion (as described in footnote 1) appeared. The results suggest that the force of exclusion in the birth season was outweighed by sexual attractiveness between individuals from different groups, and reversely in the next birth season, that is, the two contended forces were in a dynamic equilibrium across the seasons. This observation holds those on the motive of sexual attractiveness between unfamiliar animals from different groups (Japanese macaques: Enomoto, 1974; Sugiyama, 1976; rhesus macaques: Brereton, 1981; Hausfater, 1992; Tibetan macaques: Zhao, 1993), and unfamiliar opposite sexes of humans (Shepherd, 1971; Wolf and Huang, 1980) though the attractiveness was not clearly documented as a contended force of the competition in previous studies.

In conspicuous contrast with the conflicts between young immigrant males and the resident alpha male in the mating season, which produce a lot of wounds in the young adult immigrants (Zhao, 1994a), and with female-female conflicts between groups, the intergroup male-male conflict was only a ritualized show of power, which never produced any wounds. Forewarning display in this species is probably the same kind of show. Both the male-male conflict and the forewarning behavior are like by-products of female choice in mating activities within a female-banded group (Wrangham, 1980), doing so to gain the favor of females within the group.

Interrelatedly, males herding females in close encounters is typically observed in baboons (Stoltz and Saayman, 1970; Hamil-

ton et al., 1975; Cheney and Seyfarth, 1977; Cowlshaw, 1995). Such herding is thought to bar sexually receptive females from access to males in other groups (Cheney, 1987). On the other hand, sexual weight dimorphism has also been hypothesized as an important factor influencing male herding because herding is less common in less sexually dimorphic species such as Japanese macaques and vervets (Cheney, 1981, 1987). The nearly identically high rates of herding observed during intergroup encounters in the birth and mating seasons (80% and 85% respectively) rules out the cause for herding hypothesized for baboons, i.e. preventing sexually receptive females access males in other group (Cheney, 1987) because no receptive females existed in the birth season. On the other hand, when the weight dimorphism reduced from to 1.46 (*M/F*) in later winter to 1.16 in late autumn (the mating season; Zhao, 1994b), the rate of herding showed no decline. This argues against the link suggested between herding and size dimorphism (Cheney, 1981, 1987). Possibly, herding in Tibetan macaques is selected for a more subtle factor such as smoothing the males next intergroup transfer by doing so to gain the favor of females from the opposite group during encounters. Thus, attempting to gain the favor of females both within and outside the group, high-ranking males' reproductive strategies are embodied in all of the performances in intergroup interactions.

Consistent with reports on other species, the young natal males (rhesus: Hausfater, 1972; Japanese macaques: Sugiyama, 1976), and the subordinate males (vervets: Cheney and Seyfarth, 1983) were the most active participants in intergroup encounters, especially in affiliative interactions. It is also possible to consider that affiliative performances of peripheral males at the border are essential for their coming or next transfer. Thus, different tactics are used by the two classes of males in preparing their coming or next transfers in Tibetan macaques. Male intergroup transfer is closely related to raising the mating opportunity for the young immigrants, and to avoiding intermale competition for the secondary transfers that are middle-aged and old (Zhao, 1993, 1994a). In

addition to the role of couriers of genes (e.g., Nozawa et al., 1975) and culture (reviewed by Nishida, 1987; Zhao and Deng, 1992), transferring males may also go between the groups in reallocation of ranges, as that described in footnote 1.

Females were the most serious fighters in severe conflicts between groups, especially between two groups (*D-D₁* and *D-D₂*) fissioned in the recent past. This may well be related to the fact that after fission the two parts shared the same home range, and the minority was always forced to forage in the poorer parts. Interestingly, similar trend is also reported for Barbary macaque groups fissioned in the recent past (Prud'Homme, 1991), but not for Japanese monkeys (Koyama, 1970) and rhesus (Missakian, 1973), in which the relations between recently fissioned groups are initially unaggressive. In addition to the extra-development of alloparenting or male-infant caretaking [Tibetan macaques (TM): Deng and Zhao, 1996; Barbary macaques (BM): Whitten, 1987.] and male-infant-male interactions (TM: Zhao, 1996a; BM: Deag, 1980; Taub, 1980), this extrahostility between fissioned groups is likely another example of ecological factors shaping social behavior (Zhao, 1996b). Of the factors, what we know is that Tibetan (Zhao et al., 1991) and Barbary (Ménard and Vallet, 1988) macaques under poor foraging conditions feed more on foliage than other macaques, as indicated by their body weights (Clutton-Brock and Harvey, 1977; Sailer et al., 1985)—the Tibetan (Zhao, 1994b) and Barbary (Harvey et al., 1987; Fa, 1986) macaques are the largest species of their genus.

Under the given ecological conditions, fission, which occurred only in the top-ranking and largest group twice during the study period, is likely an outcome of balance between the cost of competition for food within the group, and the benefit of cooperative access to food resources for animals in the mother group. That is, when the former is outweighed by the latter, fission occurs to reduce the intra-group competition, but does not reduce the ability of the mother group to access the best feeding sites.

However, mate competition is very likely to be proximately involved with group fis-

sion because both observed fissions occurred in the mating season. Tibetan macaques can temporarily form a "far-peripheral adult subgroup" (FAS) in the mating season as a "space-segregation" tactic for mating by the loser among males and females (Zhao, 1993), thus fission may also be viewed as the development of this tactic for the daughter group.

In summary, this study first fully demonstrates the theory of sexual selection (Darwin, 1871; Trivers, 1972) with quantitative data on behavioral differences between females and males in intergroup interactions—females and males do maximize reproductive values in different way. Second, sexual attractiveness among groups is integrated/introduced into the model of the female-banded society of primates as a force contended against food competition. Third, the study groups demographic data collected with two group-fissions afford an ecological explanation of group fission.

The decline of sizes in groups A, B and D may be related to poaching that became a problem after 1987, though it stopped from time to time in the study period. (Zhao, 1994a).

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